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A contribution to the life history of Uvularia sessilifolia

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(WITH PLATES 34, 35)

INTRODUCTION

That the seasonal development of any plant, especially with reference to the unfavorable winter season, should be of interest and of some significance is undoubted. Such a study has been begun here with *Uvularia sessilifolia* and includes field observations as to growth of rhizome and aerial shoot as well as a more detailed study of the development of the megasporangium and microsporangium. The chronological development of these latter organs has received some attention, but the actual number of cases is meager, and what the significance of the history of these organs of reproduction may prove to be can be shown only after a considerable number of plants, particularly of related genera, have been studied. The variations thus far brought to light show the need of an even wider range of investigations in this line than at first would seem necessary. The plants that have been thus studied so far show a wide range of variation. *Symplocarpus foetidus* (Duggar[1]) showed the nuclei of the definitive archesporium in a resting condition about October first, with the divisions of the pollen mother cells taking place the first warm days of April. In *Trillium* (Smith[2]) the microspores were found in the mother cell stage in April together with the four potential megaspores. In *Hepatica* (Chamberlain[3]), however, the early spring, that is while the ground was still frozen, showed pollen grains fully formed and the embryo sac ready for fertilization. The same investigator[4] claimed that *Salix* passed the winter in the microspore mother cell stage with no megaspore defined till after the renewal of growth in the spring. This condition of the microsporangium has been challenged, for *Salix fragilis* (Moore[5]) showed the cells of the anther still homogeneous without differentiation of tissue in November. Perhaps *Corylus* and *Alnus*[3] gave the most extreme condition, for here the midwinter catkins showed pollen grains in which the tube nucleus and generative nucleus were distinct.

At first thought it would seem that that point which marks the end of the sporophyte generation would mark the end of the growing season. This has been made a generalization.[6] Chamberlain[3] suggests further that since the mother cell stage appears as a common halting place for the winter, this may be the condition most capable of withstanding the unfavorableness of winter. However, even the few instances given above show enough variety to lead one to suspect that perhaps the mother cell stage in winter is not to be found in a high enough majority of cases to warrant such an interpretation. The particular plant taken for this study, *Uvularia sessilifolia*, is one in which neither microspore nor megaspore passes the winter in that turning point of sporophyte and gametophyte phases.

The study is but a preliminary one and intended largely to indicate the time at which the various stages in the life history are to be sought. A cytological study of the stages here given is in progress.

COLLECTING AND METHODS

The buds of the rhizome of *Uvularia sessilifolia* were taken at intervals during the year as given below in detail. In the earlier stages the tips of the rhizome were put directly into the fixing agent, while in the later material from one to several of the bud scales were first removed. In the spring material the bud was dissected and the flower alone fixed. The fixing fluid used was chrom-acetic acid; time, twenty-four hours. The material was then washed and run through successive grades of alcohol, beginning with 15 per cent and changing the final absolute alcohol once. The infiltration was with cedar oil, 33 per cent cedar oil and absolute alcohol, 66 per cent cedar oil and absolute alcohol, and two changes of pure cedar oil. The paraffin was gradually introduced into the cedar oil and the material finally imbedded in pure paraffin melting at 54° C. The sections were cut about 7 mm. thick and mounted serially. Delafield's hematoxylin was used in staining, as only the general stages were sought.

FIELD OBSERVATIONS

Uvularia sessilifolia grows in rather close colonies, a fact correlated, of course, with the rhizome habit. The season's elongation of the rhizome appears first about the middle of April as a tiny protuberance at the base of the spring's leafy shoot. This quickly pushes out, elongating so rapidly that by the first of May the length of the new growth is one half to one inch. The growth continues very rapidly so that by the first of June the increase is from two to four inches. This is apparently almost the limit of increase. The bud at the end is at this time but slightly larger in diameter than the rhizome itself. No attempt has been made in this study to get at the contents of the buds borne at the base of the flowering and the non-flowering branches. The tip end becomes curved upward slightly and is usually at depths varying from one to three inches below the surface of the ground. The size of the bud increases mostly during the latter part of August and the month of September. From October through to March the size is practically the same. With the renewal of growth in the spring, however, the portion just back of the bud again elongates rapidly and the buds increase greatly in diameter and length so that they appear above ground about the middle of April, those containing flowers being about one fourth of an inch in diameter. The flowers appear the first week of May.

An interesting and probably very significant fact is noticed in connection with those plants having flowers. In all the plants observed the flowering plant is seen to branch once, the flower being borne at the first or second node of one of the branches. Conversely, no plant was found branched that did not blossom. This reminds one of similar occurrences in *Erythronium* and in *Podophyllum*, where the flowering plant bears in every instance two leaves, the non-flowering ones a single leaf.

DEVELOPMENT OF THE MICROSPORANGIUM

The development of the microsporangium is the usual one throughout, as will be seen in the stages here given. The first stage which I obtained for the microsporangium is that seen August 8, in which the inner whorl of stamens shows the differentiation of the hypodermal cell with beginnings of divisions into primary wall and primary sporogenous cell, FIG. 1, while the outer whorl of stamens has advanced to show several divisions of the primitive sporogenous cells as well as of the wall cells, FIG. 2. The general four-lobed appearance of the younger set is seen by reference to FIG. 3, and the comparative advance of the outer whorl noted in FIG. 4. (The crowding of the stamens is particularly noticeable at this time, which would account for the irregularity of outline in FIG. 4.) This earlier development of the outer set of stamens is noted in the history of the development until at the time of tetrad formation, the two are very nearly synchronous. The stages of the individual cells throughout any single anther are practically simultaneous.

The differentiation of the hypodermal cell is the usual one, namely, the increased size and denser cytoplasm, FIG. 5. The number of primary archesporial cells may be from three to six, FIG. 1, 2. In the young sporogenous cells the chromatic material is apparently very abundant, irregularly distributed in the fine linin mesh with prominent knots at the crossings. Two nucleoli are noted as of frequent occurrence, a condition that persists up to the mother cell stage, FIG. 5. The tapetal cells were not differentiated at this stage.

The primary wall cells divide to form five layers, the three outermost making up the permanent wall of the sporangium, FIG. 6, the innermost functioning as tapetum, while the intervening one breaks down at the time of maturity of the microspore mother cells. The tapetal jacket cells round off with the sporogenous mass, and at the time just preceding synapsis are usually elongated, the nuclei all in the end next the sporogenous tissue, FIG. 7. The nuclei of the tapetum are apparently at this time about to disorganize, staining diffusely and appearing as dark masses.

The mature spore mother cells, seen about the middle of September, have so increased in size that the prominent nucleus is now the size of the original hypodermal cell. The linin network of the nucleus is finer and the chromatin more evenly distributed, although still prominently knotted, than in the primitive sporogenous cells. The nucleolus (frequently two appear) is prominent. By the latter part of September the spore mother cells of the outer whorl of stamens show synapsis.

The material collected October 21, 1910, and that collected October 27, 1909, show the formation of tetrads, the phases varying from the equatorial plate stage of the heterotypic division to the complete organization of the four daughter nuclei. The usual large thick chromosomes that characterize the reducing division are seen. At the end of this division a resting nucleus is formed in each of the daughter cells, but no wall separates the two. The homoeotypic division, however, is not long delayed, as in the same anther all these stages may be found including the completed tetrads.

The spores round off and increase in size; it is at this point that the approach of winter is met. With the renewal of growth in the spring the pollen grains found in early March show the outer and inner walls differentiated and apparently mature in size. In this early spring condition the nucleolus is prominent, and the linin mesh fine and close with small chromatic granules. The division of the pollen grain nucleus into tube and generative nuclei is noted in the late April material, in which the generative nucleus appears not fully organized but showing traces of the spireme condition, and the tube nucleus is characterized by a large nucleolus but poorly organized reticulum, FIG. 8. The generative nucleus is rich in chromatic material staining deeply, and the tube nucleus has but little. I have not found the division of the generative nucleus, which evidently takes place after the shedding of the pollen.

DEVELOPMENT OF THE MEGASPORANGIUM

Turning to the study of the megasporangium, we find that its development is as tardy as that of the microsporangium is early. At the time when the archesporium of the microsporangium is formed, the ovary is a homogeneous mass. In September the carpelary cavities have appeared, and in each a pair of nucelli are protruding. The number of these cell masses destined to develop the megasporangia varies from two to three pairs for each cavity. In general each of a pair is on the same plane. In October and even as late as December the uniformity of the nucellar tissue is unchanged, and very little change in size is noted, FIG. 9 and 10. In early March the outline of the nucellus is such as to suggest an enlarging hypodermal cell at the side next the carpel wall, FIG. 11. The cells of the hypodermal layer, however, do not show the characteristics of the usual archesporial tissue, for the cells are only slightly enlarged, the cytoplasm not dense, and the chromatic network not prominent. Moreover, more than one of the hypodermal cells show a slight increase in size, perhaps indicating the archesporial potentiality of several hypodermal cells, FIG. 12. This is indicative of a primitive condition. A single cell, however, increases more rapidly than the others, getting a start over the others, for in the material of March 14 this greater increase is noted in the cell destined to develop the embryo sac, FIG. 13.

By the first of April this enlarging cell has become quite prominent, giving the cell mass a decidedly one-sided appearance. The nucleus is large but still with inconspicuous reticulum. This cell continues to increase in size, FIG. 14, and toward the end of April projects strongly, and the inner integument has begun to develop. The nucleus at this stage shows synapsis, indicating that the hypodermal cell does not divide to cut off a primary wall cell but functions directly as the megaspore mother cell, FIG. 15.

Five days later, April 30, the turning of the ovule, which was slight on April 25, is now almost complete and the ovule typically anatropous. The integuments have grown rapidly and almost surround the embryo sac. Owing to the twisting of the ovule at this time, it has been found difficult to obtain a longitudinal section of the developing mother cell. However, in material collected May 7 the division of the mother cell, which was in synapsis one week earlier, is complete, and two cells, which may be called megaspores, are seen. Vesque[7] has stated that each develops an embryo sac to the four-nucleate stage.

SUMMARY

1. The archesporium of the microsporangium, consisting of from 3 to 6 hypodermal cells, becomes differentiated the first of August.

2. The hypodermal cells divide at this time forming the primary sporogenous and the primary parietal cells.

3. The primary parietal cells divide several times, giving rise to the permanent wall of the sporangium and to the tapetum.

4. The primary sporogenous cells give rise to several microspore mother cells which are found mature in the middle of September.

5. The divisions of the microspore mother cells take place in October and show the usual tetrads. The winter is thus passed with microspores fully formed.

6. In the latter part of April the microspore divides to form the generative and the tube nuclei. The division of the former probably occurs after the shedding of the pollen.

7. The archesporium of the megasporangium is not differentiated till early March and consists of a single hypodermal cell, the adjacent cells showing gradations in size and characteristics of potential archesporial cells.

8. The archesporium does not divide to form a primary wall cell and primary sporogenous cell but functions directly as the megaspore mother cell. It reaches maturity about the middle of April.

9. The reduction division of the megaspore mother cell takes place the last week of April.

10. Two megaspores are found about one week later.

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Explanation of plates 34, 35

Uvularia sessilifolia

All drawings have been made with the aid of a Bausch and Lomb microscope and camera lucida.

PLATE 34

FIG. 1. Portion of cross section of anther of inner stamen of flower on August 8. (× 310.) *H*, hypodermal cell. *D*, hypodermal cell dividing into primary sporogenous and primary wall cell. Three hypodermal cells apparently give rise to archesporium.

FIG. 2. Portion of cross section of anther of outer stamen of flower on August 8. (× 310.) *D*, derivatives of primary wall cell. *P*, primitive archesporium. Five hypodermal cells apparently divided.

FIG. 3. Outline of cross section of inner anther of flower on August 8. (× 70.)

FIG. 4. Outline of cross section of outer anther of flower on August 8. (× 70.)

FIG. 5. Single hypodermal cell of anther on August 8. (× 720.) Note two nucleoli.

FIG. 6. Portion of cross section of anther on September 21. (× 70.) *W*, wall cells, 3 layers. *M*, middle layer, disappearing. *T*, tapetum. *S*, microspore mother cells.

FIG. 7. Portion of cross section of anther, September 27. (× 310.) *S*, microspore mother cell. *T*, tapetum cells elongated, nuclei close to spore mother cells. *M*, middle layer disorganized. *W*, wall.

FIG. 8. Cross section of pollen grain, April 25. (× 720.) *G*, generative nucleus. *T*, tube nucleus: note the prominent nucleolus and poor reticulum.

FIG. 9. Outline of portion of cross section of ovary showing two nucelli, Oct. 21. (× 70, material somewhat shrunken.)

PLATE 35

FIG. 10. Outline of portion of cross section of ovary showing two nucelli, Dec. 8. (× 70, material somewhat shrunken.)

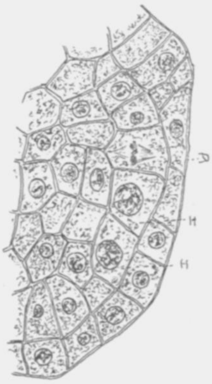
FIG. 11. Outline of portion of cross section of ovary showing nucellus with slight swelling at one side, Mar. 3. (× 70.)

FIG. 12. Portion of longitudinal section of nucellus, showing enlarging hypodermal cells, Mar. 3. (× 310.) *M*, probable megaspore mother cell.

FIG. 13. Portion of longitudinal section of nucellus, showing megaspore mother cell enlarging, Mar. 14. (× 310.)

FIG. 14. Portion of longitudinal section of nucellus showing megaspore mother cell, April 13. (× 310.)

FIG. 15. Portion of longitudinal section of nucellus, showing nucleus of megaspore mother cell in synapsis and origin of inner integument, April 25. (× 310.)



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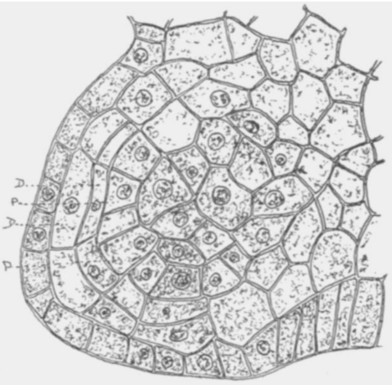

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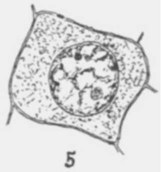

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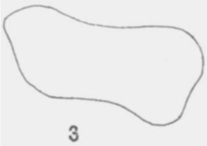

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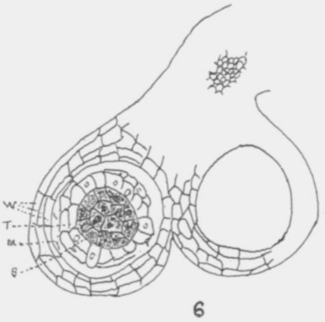

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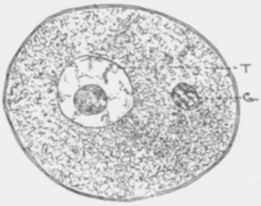

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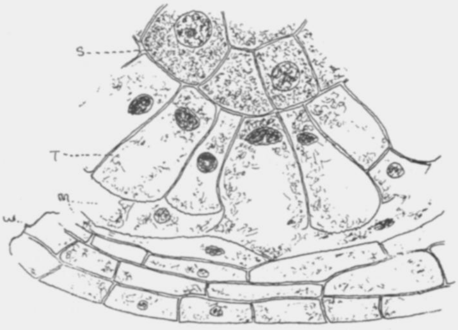

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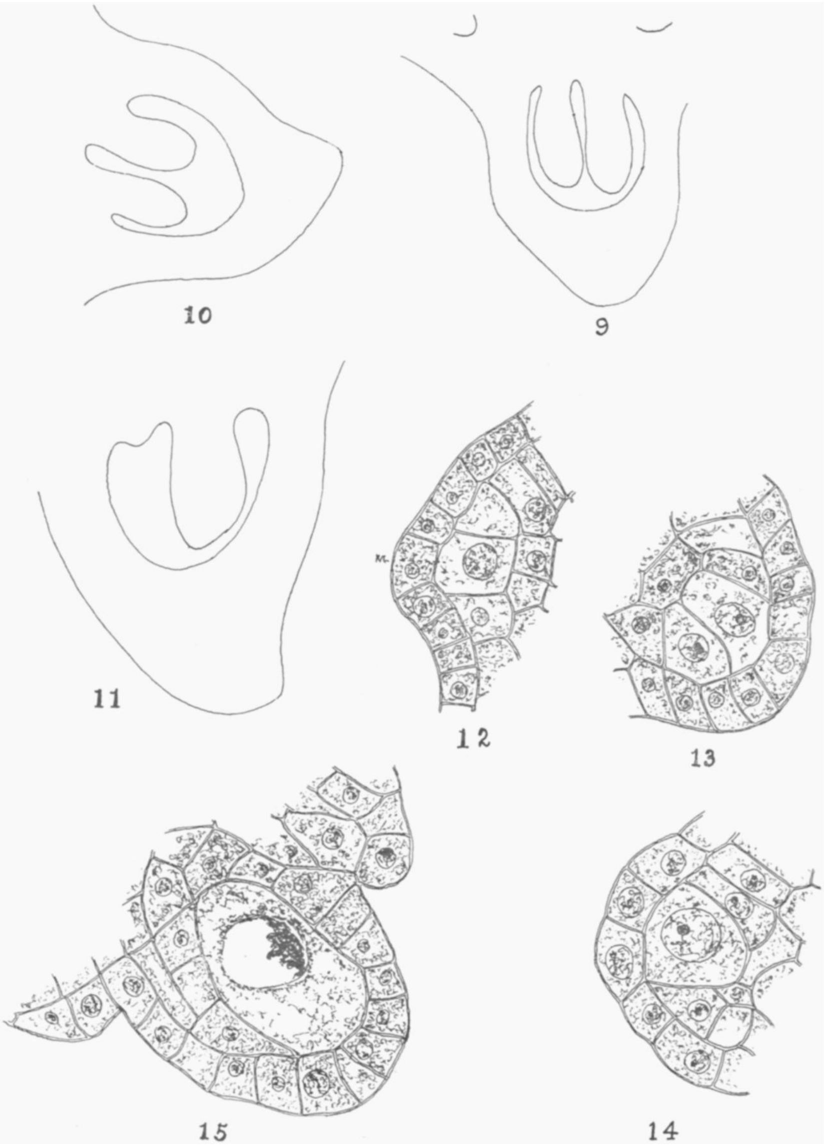

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